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On a New Species of the *Virilis* Group of the Genus *Drosophila*
(Diptera, Drosophilidae), with Revision of the Geographical
Distribution of the Group

With 4 Text-figures

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ABSTRACT A new species of the genus *Drosophila*, *D. kanekoi*, sp. nov., is described. A morphological comparison is made of the spermatheca, a female reproductive organ, in the *virilis* group, from the viewpoint of character phylogeny. The geographical distributions of the members of this group are summarized and discussed in relation to the evolution of the group.

INTRODUCTION

To date, about 200 drosophilid species have been known in Japan (Okada, 1956; Takada, 1971; Beppu *et al.*, 1977). Of these, two species belong to the *virilis* species-group, which is supposed to have originated in Asia as a group of temperate deciduous forest (Patterson and Stone, 1952; Throckmorton, 1975).

During our ecological survey, an unknown species belonging to this group was collected at several localities in Hokkaido and in northern Honshû. This species morphologically resembles *D. littoralis* Meigen, distributed in Europe. Moreover, two other species of this group were collected, both of which are new to Japan.

Firstly, the present paper deals with a description of the new species, which is named *D. kanekoi* in honor of Dr. Akashi Kaneko, Japanese Ministry of Education, in comparison with *D. littoralis* from Finland. Secondly, the morphology of the spermathecae, which vary species-specifically, is compared among the members of the group. Thirdly, much of the available information obtained recently on the geographical distribution is summarized and discussed in relation to the evolutionary history.

Drosophila kanekoi sp. nov.

[Japanese name: Futokuro-shôjôbae]

Drosophila sp. 4, Beppu *et al.*, 1977.*External characters of imagines*

Male and female: Body dark brown. Body length (in live specimen) about 3.8 mm in male and 4.0 mm in female. Wing length 3.3 mm in male and 3.5 mm in female. Head color and chaetotaxy as in *littoralis*. Antennae dark, arista with 7–8 branches including a small fork, 2 branches below it.

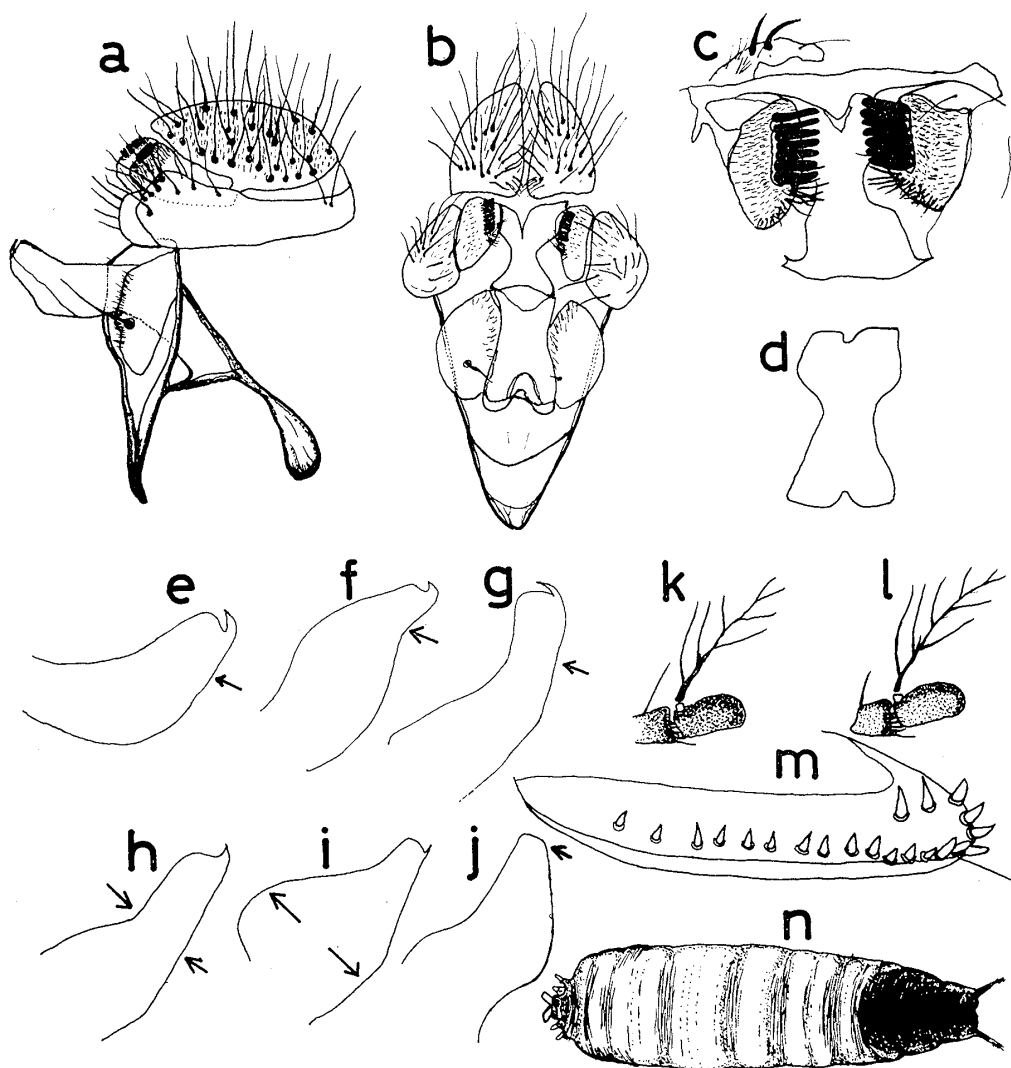


Fig. 1. *Drosophila kanekoi* sp. nov. Male genitalia in side view (a) and in ventral view (b). Surstyli (c) and decasternum (d). Penis in side view, of *D. kanekoi* (e), *D. littoralis* (f), *D. montana* (g), *D. lummei* (h), *D. virilis* (i) and *D. ezoana* (j). Aristae of *D. kanekoi*, with 7 branches (k) and 8 branches (l). Egg-guide (m) and pupa (n) of *D. kanekoi*.

Front brownish, about $5/7$ as broad as head-width. Carina high, narrow and sulcate. Cheek about $1/4$ as broad as the greatest diameter of eye. Eyes dark red. Second oral bristles about $1/3$ – $2/5$ of vibrissae.

Mesonotum brownish black as in *virilis* and somewhat darker than in *littoralis*, with brown longitudinal stripes within the dorsocentral rows. Acrostical hairs in 6 rows. Cross distance of *dc* about 0.75 times the length. Legs pale brown. Preapicals on all three tibiae. Abdomen dark brown, somewhat lighter on basal segment in mid-line as in *littoralis*, but more roundish in shape than in *littoralis*. Wings slightly dusky, posterior crossveins with narrow dark cloud; anterior not cloudy. Two stout bristles at distal costal break. Halteres yellow. Costal index about 3.0; 4th vein index about 1.3; 5X index about 1.3; 4C index about 0.8. Third costal section with heavy bristles on basal $3/5$. Male genitalia as shown in Fig. 1. Surstyli with 8 dark teeth as a rule. The decasternum as in *littoralis*. Penis in side view different from that of *littoralis* or *montana* (Fig. 1 e–g). Ovipositor as shown in Fig. 1 j. The number of teeth along the ventral margin of the egg guide varies with individuals, ranging from 14 to 18. This is not a reliable characteristic for distinguishing the species in the group.

Internal characters of imagines

General features of the male reproductive organs as in *littoralis*. Ejaculatory bulb of the male very small. Testes in mature male dark red. The spermatheca of the female is characteristically different from those of the other members (cf. Fig. 2 and Remarks 1). Ventral receptacle with 150 loose coils.

Other characteristics

Egg:— four filaments.

Larva and pupa:— The larvae tend to pupate either on or just above the surface of the medium in a culture bottle. The freshly formed pupa is white, soon turns red firstly at the front part, and finally becomes tannish red. The horns are short. The pupa closely resembles those of *montana* and *littoralis* in its shape and coloration.

Distribution and ecology

Distribution:— Hokkaido, Tōhoku, and Hokuriku, northern Japan.

Habitat:— *Drosophila kanekoi* is restricted to the high humidity belt along streams, like other members of this group (Beppu, pers. comm.). A few individuals are often collected at timberyards in Tōhoku, together with a large number of *D. virilis*.

Food:— Unknown but probably associated with the tree-sap of the willow.

Holotype:— The holotype and three paratypes (River Chitose near Sapporo, June, 1977) are deposited at Hokkaido University along with slides of the male genitalia, egg-guides and wings.

Stocks:— The species is easily maintained in stocks. Two isofemale lines

from Chitose in Hokkaido and from Kirioka in Honshû are cultured in our laboratory.

Notes

The females of *D. kanekoi* is easily distinguishable from all the other members of this group by its spermathecae (cf. Fig. 2), and the male generally by its penis in side view (Fig. e-j). In particular, this species is sympatric with *D. ezoana* in some localities. Unlike *D. kanekoi*, the penis of the latter has no hook at the tip (Takada and Okada, 1956).

REMARKS

1. *Morphology of spermathecae**

In general, the species in the *virilis* group show a similar external morphology under the stereoscopic binocular microscope, and therefore, the considerable differences in the spermathecal shapes are a more reliable criterion for distinguishing the species (Throckmorton, 1962; Kurokawa, 1972).

Although it is difficult to arrive at any firm conclusions regarding the primitive type or the phylogeny, a hypothetical character phylogeny of the spermathecae (Fig. 3) may be constructed on the basis of information from salivary gland chromosomes and proteins (Stone *et al.*, 1960; Throckmorton, 1978).

Four species in the *montana* sub-phyad have very similar spermathecae, which are bell-shape in general appearance. Moreover, each of the spermathecal ducts expands to form a small bulb just prior to its union with the introvert (Fig. 2 j-m). Pigmentation of the spermathecae of grown-up females varies among geographical strains of *D. montana*, although it changes with adult age. The Finnish and Japanese *D. montana* have darker spermathecae than the North American form (Fig. 2 f and j). The spermathecae of *D. lacicola* resemble those of its sibling *D. montana*, except for the length of the duct in the capsule and the presence of small wart-like spines on the apical surface. Those of *D. flavomontana* have a small apical indentation. *D. borealis* has pear-like spermathecae with horizontal stripes on the basal half of the outer surface.

Dorosophila ezoana is genetically more isolated than any other members of the group (Stone *et al.*, 1960). Similarly, its spermathecae are the most different, being almost quadrate in profile with a small apical indentation like *D. flavomontana* and large wart-like spines distributed nearly all over the upper half of the outer surface (Fig. 2). *D. littoralis* has spermathecae with very small spines on the upper surface and characteristically with oblique stripes almost covering the basal half.

Of the five species in the *virilis* phylad, *D. virilis*, *D. novamexicana* and *D. americana* have spherical to oval spermathecae which are strongly wrinkled and constricted at the base (Fig. 3, arrows). Those of *D. lummei* are of simpler struc-

* For convenience of reference, the term spermathecae is here used to refer to the inner capsule only.

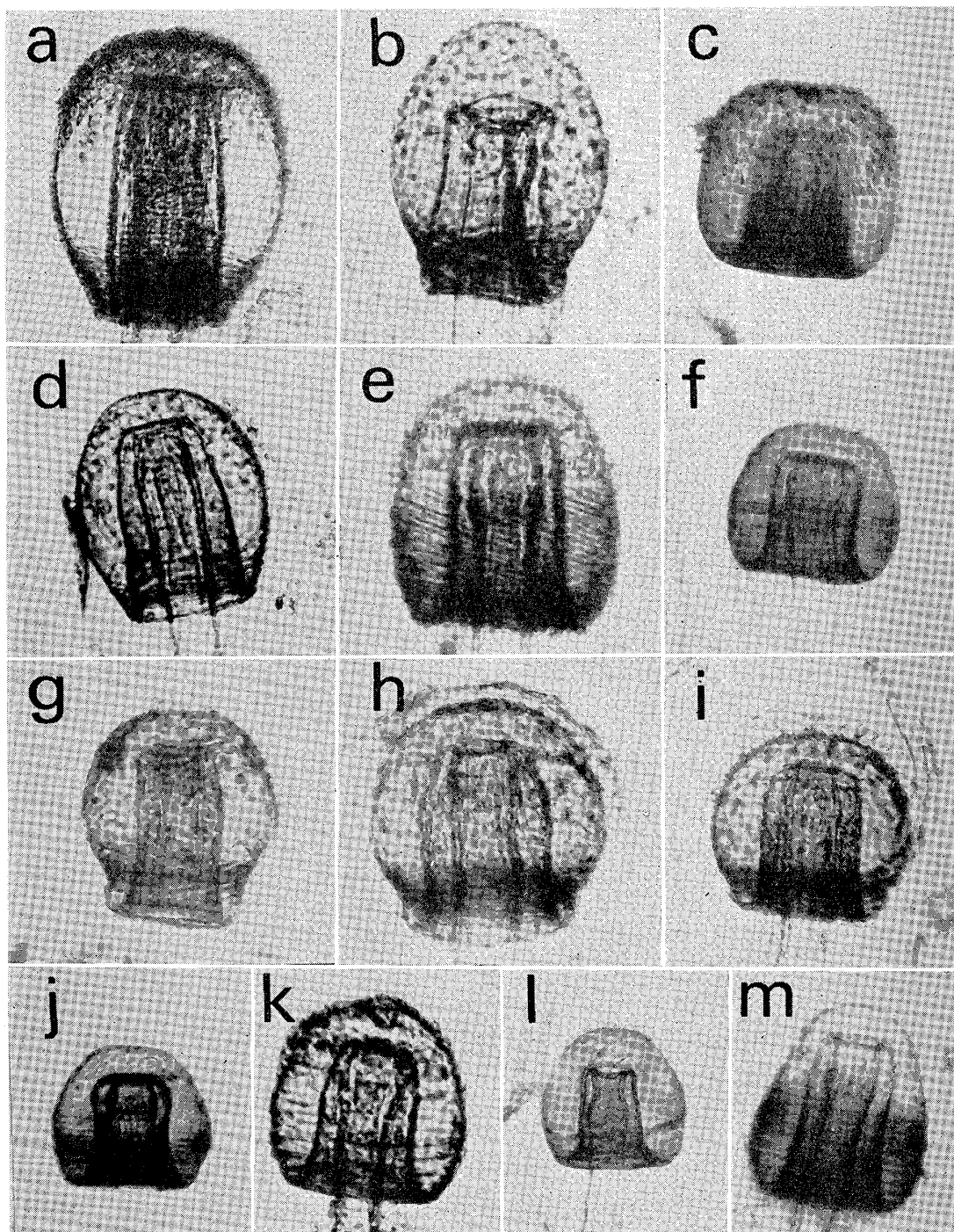


Fig. 2. Spermathecae in the *virilis* group. *D. kanekoi* (a), *virilis* (b), *ezoana* (c), *lummei* (d), *littoralis* (e), Finnish *montana* (f), *texana* (g), *novamexicana* (h), *americana* (i), North American *montana* (j), *flavomontana* (k), *laticola* (l) and *borealis* (m).

The spermathecae were treated with 15% KOH to remove the spermathecal envelopes.
a, ca. $\times 250$; b-m, ca. $\times 300$.

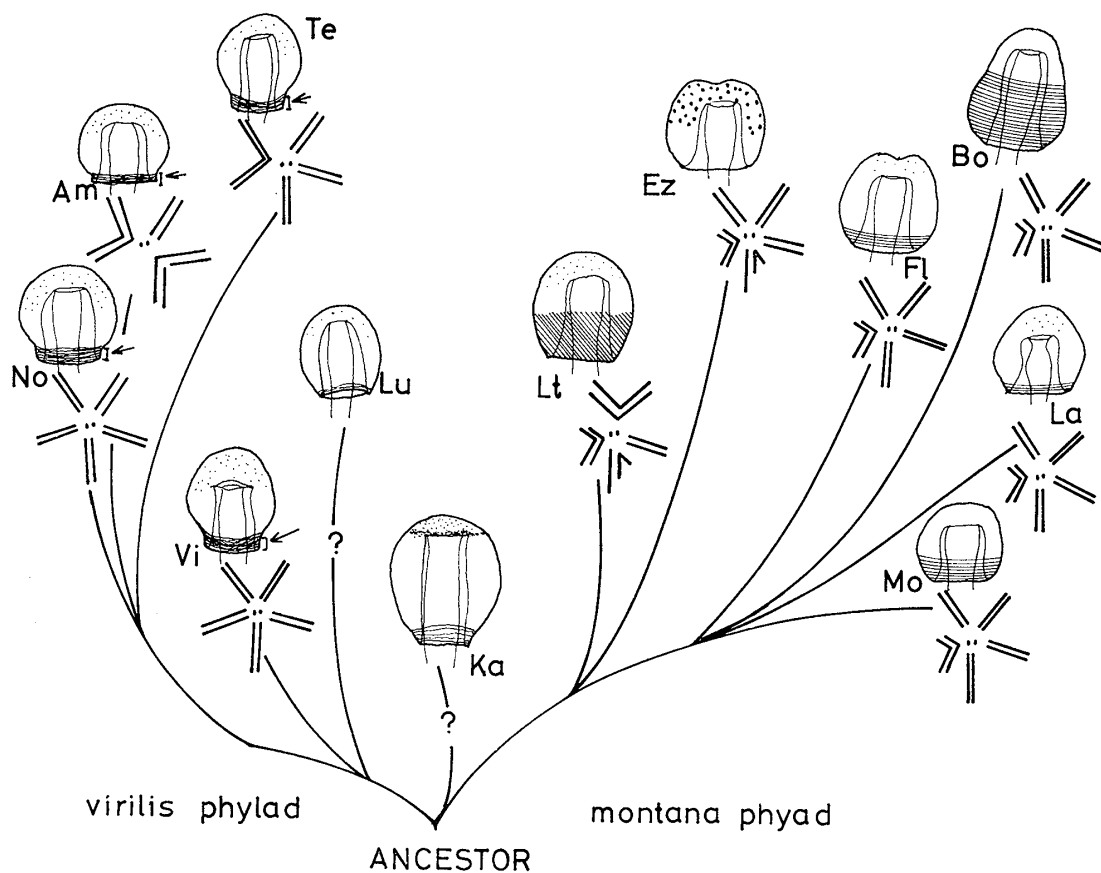


Fig. 3. A hypothetical character phylogeny of spermathecae, based on the chromosomal phylogeny (Stone *et al.*, 1960). Abbreviations are: Vi, *D. virilis*; Lu, *D. lummei*; No, *D. novamexicana*; Te, *D. texana*; Am, *D. americana*; Ka, *D. kanekoi*; Lt, *D. littoralis*; Ez, *D. ezoana*; Mo, *D. montana*; La, *D. laticola*; Fl, *D. flavomontana*; Bo, *D. borealis*.

ture, elongate oval, and are not constricted, unlike the remainder of this phylad. *D. kanekoi* has similar spermathecae. Its spermathecal ducts enter deeply into the capsule as in *D. lummei*. Throckmorton (pers. comm.) suggests that *D. kanekoi* might be an early member of either of the two major phylads or be the first species of the *montana* phylad in the chromosomal analysis. As regards comparative morphology of the spermathecae, *D. kanekoi* is most closely related to *D. lummei* of the *virilis* phylad. On the other hand, non-constricted spermathecae are found in *D. littoralis*, in *D. ezoana* and in the *montana* sub-phylad, although their shapes differ in outline from species to species. Furthermore, *D. kanekoi* is allied to *D. littoralis* in its general external features and to *D. montana* in crossability (unpubl.). This species has characteristics in common with both the *virilis* and the *montana* phylads. These facts indicate that the elongate oval spermathecae might be a more primitive form in the *virilis* species-group. Information on the comparative morphology of spermathecae, to some extent, corresponds to the phylogeny based on chromosomes and proteins.

2. Distribution of the *virilis* group

The geographical distribution of the members of the *virilis* group is of importance in considering the evolution of the group. This group presently comprises twelve species including the new species described above, and is exclusively found in the Palearctic and Nearctic Regions. *D. virilis* is the widely distributed member and occurs in four different zoogeographical realms (Patterson and Stone, 1952; Bock, 1976). However, it is a cosmopolitan domestic species and its wide range of distribution is due to human transportation (Dobzhansky, 1965). The species *D. virilis* itself is regarded as having originated in the eastern Palearctic or Oriental Region (Patterson and Stone, 1952; Throckmorton, 1975). Until recently, a great majority of the members were considered to be endemic to a single zoogeographical region. Seven species, three closely related species in the *virilis* phylad and four in the *montana* complex, were regarded as North American forms. *D. littoralis* and *D. lummei* were recorded exclusively in Europe. *D. ezoana* was the only wild species of the group endemic to Japan. In the last five years, however, new information on the distribution has been accumulated by Finnish and Japanese workers.

Lakovaara and his collaborators (1974) noted that *D. ezoana* is also present in Norway, Sweden and Finland. The species *D. montana* had been believed to be restricted to the Rocky Mountain System since its description by Stone and his co-workers in 1958. However, Lakovaara and Hackman (1973) reported this species (as *D. ovivororum*, synonym) from the Scandinavian countries. Kaneko and Watabe (unpubl.) have collected *D. montana* and *D. lummei* in Japan. The latter was previously recorded from the Scandinavian countries alone (Hackman, 1972). This recent information, together with the discovery of a new species, *D. kanekoi*, from Japan, must greatly contribute to evolutionary studies of this

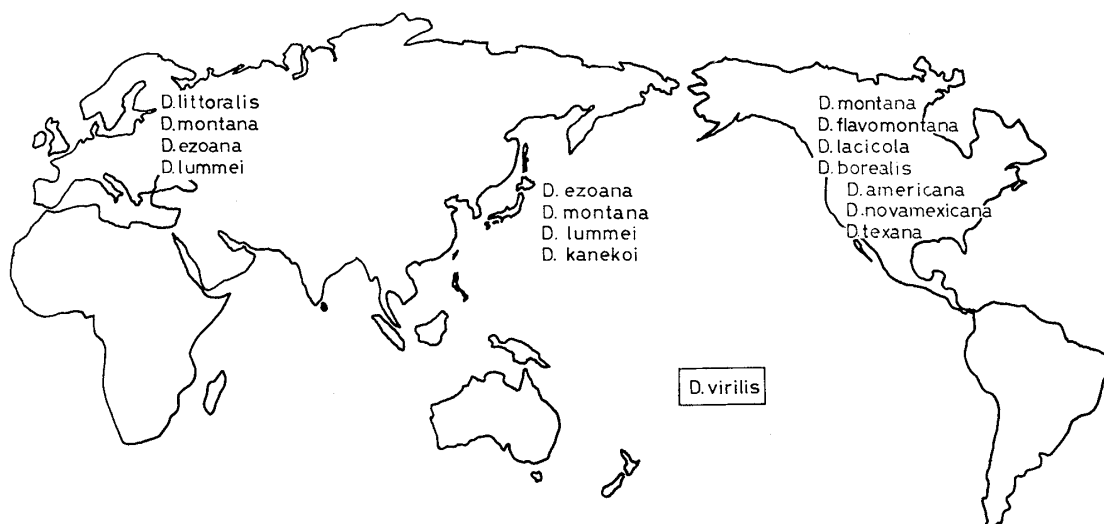


Fig. 4. Geographical distributions of the members in the *virilis* species-group.

group. The geographical distribution of the group is redrawn in Fig. 4, on the basis of such recent discoveries.

According to the chromosomal analysis by Patterson, Stone and their colleagues, it seemed that *D. virilis* would be the nearest to the hypothetical ancestor in the phylogenetic relationship. However, any species which are very closely related to the ancestral form or *D. virilis* itself have not been found in East Asia. *D. americana*, *D. texana* and *D. novamexicana* are genetically related to *D. virilis* but these three are all restricted to North America.

Such a disjunctive pattern in the distribution has made it difficult to trace the evolutionary processes of speciation. Recently, Throckmorton (1978) found that *D. lummei* was most closely related to *D. virilis*, and as mentioned above, this species has been known to spread in East Asia where *D. virilis* is supported to have been native. Moreover, the new Japanese species *D. kanekoi* has some primitive morphological characteristics common to the two major phylads (cf. Remarks 1). These facts prove that early speciation of this group would have occurred in the East Palaearctic or Oriental Region.

Genetic analyses are being made by crosses between *D. kanekoi* and other members of this group. The details will be published in the near future.

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